

Genetic Variability for Mineral Element Concentrations of Wild Jerusalem Artichoke Forage

Gerald J. Seiler* and Larry G. Campbell

ABSTRACT

One of the potential uses of Jerusalem artichoke (*Helianthus tuberosus* L.) is as a forage crop. Information on inherent differences in forage nutritional quality is essential if the quality of the forage is to be improved through breeding. The objectives of this study were to determine the genotypic variability among and within wild Jerusalem artichoke populations for the concentration of N, P, Ca, Mg, K, and the Ca/P ratio in the forage at flowering, estimate the magnitude of genotype \times environment interaction, and examine relationships among mineral concentrations in the forage. Nine wild Jerusalem artichoke populations grown in an irrigated field nursery at Bushland, TX, were evaluated for N, P, Ca, Mg, K, and the Ca/P ratio in the forage at flowering over a 2-yr period. Population, year \times population, and error variances were estimated to calculate the phenotypic variance. Estimates of the within-population variances were also determined. The adequacy of Jerusalem artichoke forage at flowering for maintenance of a ruminant animal was classified as follows: N, Ca, Mg, and K as adequate, P inadequate, and the Ca/P ratio as excessive. There were genotypic differences among the nine populations for N, K, P, Ca, Mg, and the Ca/P ratio for both years and averaged across years. The magnitude of the genotypic variance components indicated that a substantial proportion of the total variation for these elements was due to genotype, indicating the possibility of improvement through hybridization and selection. Within-population variation for N, Ca, and K was high, indicating potential for improvement with further selection within populations. Population variances for P and Mg were low, suggesting it will be difficult to improve these with selection. Unfortunately, P is inadequate in the forage to begin with, and our data indicated that selecting within populations for high P may not be very successful.

JERUSALEM ARTICHOKE, a perennial species native to North America, is often present as a weed in pastures (Crawford et al., 1969) and crops (Wyse et al., 1986; Wall et al., 1986) in the USA. Plants regenerate from rhizomes (tubers), which persist in the soil and make their control in subsequent crops more difficult. It has been evaluated as a potential biomass source (Swanton and Cavers, 1989) and as an alternative sweetener, storing carbons as linear fructose polymers (fructans) and inulin (Schittenhelm, 1999; McLaurin et al., 1999). Jerusalem artichoke has been used as a suitable livestock feed since the mid-1600s, especially in Europe (Cosgrove et al., 2000; Kosaric et al., 1984). Promotional claims have been made concerning the North American Jerusalem artichoke crop as a livestock feed, but only meager information is available concerning its nutri-

tional value and the variability of nutrients among and within wild species populations (genotypes).

If Jerusalem artichoke is to be used as a silage-forage crop, nutritional information about whole plants is essential. Seiler (1988) found that whole plants of wild and cultivated Jerusalem artichoke populations had a crude protein of 60 to 90 g kg⁻¹. This is adequate for maintenance of ruminant animals (National Academy of Sciences, 1984). Nutritionally adequate amounts of Ca, Mg, and K were present in whole plants at flowering, but the P concentration was suboptimal (<2 g kg⁻¹) for ruminants.

The existence of genetic variability in mineral element composition would indicate the potential for selecting for enhanced forage quality. Limited information is available about the genetic variability for the concentrations of key elements (Seiler, 1988; Somda et al., 1999), but no information is available on the heritability of these elements and the potential to breed for specific elements. The objectives of this study were to: (i) determine the genotypic variability among and within wild Jerusalem artichoke populations for the concentration of N, P, Ca, Mg, K, and the Ca/P ratio in their forage at flowering, (ii) estimate the magnitude of genotype \times environment interaction effects, and (iii) examine relationships among mineral concentrations in the forage.

MATERIALS AND METHODS

Nine populations of wild Jerusalem artichoke, a native perennial, were established by planting rhizomes (tubers) in a nursery at Bushland, TX, on a Pullman clay loam soil between 1979 to 1982 (Table 1). The nursery was fertilized with 56 kg N ha⁻¹ in the spring of each year. Plants were furrow irrigated to maintain maximum plant growth. The experimental design was a randomized complete block with three replicates. Plots were 1.5 by 7.5 m with a plant population of 50 plants plot⁻¹ (45 000 plants ha⁻¹). Weeds were controlled mechanically and by hand-hoeing.

Since wild Jerusalem artichoke plants are branched, multi-headed, and flower over several weeks, the flowering stage was defined as the time when one-half of the heads in a plot were flowering (at anthesis). This is equivalent to the R-5.5 stage in cultivated sunflower (Schneiter and Miller, 1981).

Herbage of nine randomly selected plants from the middle of the plot was hand harvested at ground level at flowering in 1983 and 1984. Forage samples were dried in a forced air oven at 65°C for 48 h, ground in a Wiley mill to pass through a 1-mm screen, and stored in sealed plastic vials before chemical analysis for N, P, K, Ca, Mg, and calculation of the Ca/P ratio.

Total N was determined by the Kjeldahl method (Jackson, 1958). A nitric, perchloric, and sulfuric acid (3:1 v/v) digestion of 1 g of forage sample preceded analysis for K, Ca, Mg, and P analyses (Jones and Steyn, 1973). Potassium, Ca, and Mg were determined by atomic absorption spectrophotometry (Isaac and Kerber, 1971), and P by the aminonaphthosulfonic acid method on an auto analyzer (Technicon Corporation,

USDA-ARS, Northern Crop Science Laboratory, PO Box 5677, Fargo, ND 58105, USA. Received 28 Oct. 2002. *Corresponding author (seilerg@fargo.ars.usda.gov).

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Table 1. Wild Jerusalem artichoke populations examined for mineral elements.

Population	PI number	Origin
Texas-1	435891	Nocona, TX
Texas-2	435892	Kilgore, TX
Illinois	435894	Milford, IL
Minnesota-1	—	Moorhead, MN
Minnesota-2	—	Detroit Lakes, MN
Iowa-1	—	Sioux Rapids, IA
Iowa-2	—	Storm Lake, IA
Iowa-3	—	Jefferson, IA
South Carolina	—	Bamberg, SC

1968). Samples for K, Ca, and Mg were prepared in 0.1% (w/v) lanthanum (La) before analysis (Hanlon, 1992).

Two hundred forty-three samples (9 plants \times 3 replicates \times 9 populations) were analyzed for mineral content each year. The mean value for the plants in a plot was used in an analysis of variance (ANOVA) for each year and across years to determine population differences and the significance of the population \times year interactions. Populations, replications, and years were considered to be random effects. Variances due to populations (σ_p^2), the interaction of year and population (σ_{py}^2), and error (σ_e^2) and their standard errors were calculated from the mean squares of the ANOVAs, by standard methods (Becker, 1984). The phenotypic variance (σ_p^2) was calculated by the following equation:

$$\sigma_p^2 = \sigma_g^2 + \sigma_{gy}^2 + \sigma_e^2 \quad [1]$$

Estimates of within-population variances (σ_w^2) were determined for N, P, K, Ca, Mg, and the Ca/P ratio. An ANOVA was conducted for all populations within a year with the individual plant data. One population was then deleted and the ANOVA was repeated on the modified data set. The within-population sum of squares for the deleted populations was determined by subtracting the within-population sum of squares of the deleted data set from the within-population sum of squares of the complete data set. The within-population variance for the population was determined by dividing the within-population sum of squares by the within-population degrees of freedom. This process was repeated for all nine populations for both years for a total of 18 ANOVAs for each element. Pearson correlation coefficients were determined among pairs of elements using individual plant data from both years.

RESULTS AND DISCUSSION

Variation among Populations

There were genotypic differences among the populations of Jerusalem artichoke for forage N and K concentrations (Table 2). When averaged across years, popula-

Table 2. Summary of analysis of variance for mineral element concentrations of wild populations of Jerusalem artichoke grown at Bushland, TX, in 1983 and 1984.

Mineral element	Statistical significance of mean squares		
	Populations		P \times Y†
	1983	1984	Across years
N	**	**	**
P	**	**	**
Ca	**	**	**
Mg	**	**	**
K	**	**	**
Ca/P	**	**	**

** Indicates significance at the $P = 0.01$ level of probability based on F test.

† P \times Y = Population \times year interaction effect.

‡ NS = Not significant at $P = 0.05$ based on F test.

Table 3. Mean and range of values of individual plants for mineral element concentrations and the Ca/P ratio in forage of wild Jerusalem artichoke populations grown at Bushland, TX, in 1983 and 1984.

Mineral element	1983		1984	
	Mean \pm SE	Range	Mean \pm SE	Range
g kg ⁻¹				
N	12.6 \pm 0.2	6.6–18.5	12.8 \pm 0.2	6.8–18.6
P	1.4 \pm 0.1	0.8–2.4	1.4 \pm 0.1	0.9–2.4
Ca	19.3 \pm 0.5	8.5–37.2	20.2 \pm 0.5	8.8–39.1
Mg	2.7 \pm 0.1	1.6–3.6	2.7 \pm 0.1	1.7–3.6
K	15.2 \pm 0.2	9.9–21.4	15.3 \pm 0.2	9.8–21.8
Ratio				
Ca/P	16.5 \pm 0.6	4.3–33.7	16.7 \pm 0.6	4.4–34.3

tion \times year (P \times Y) interactions were nonsignificant for N and K, indicating that the populations had a similar ranking in both years. There were also genotypic differences among the populations for P, Ca, Mg, and the Ca/P ratio for both years and averaged across years. When averaged across years, there was a significant P \times Y interaction, i.e., the populations did not rank similarly in P, Ca, Mg, and the Ca/P ratio over the two years.

Recommended mineral concentrations of forages for ruminants vary by age, sex, and physiological condition of the animal (National Academy Sciences, 1984; Reid and James, 1985). In terms of mineral requirements for the maintenance of a ruminant animal, forage of Jerusalem artichoke harvested at flowering can be classified as follows: N adequate, P inadequate, Ca adequate, Mg adequate, K adequate, and the Ca/P ratio as high (Table 3).

Rations with the most efficient utilization of Ca and P by ruminants are those with Ca/P ratios between 1:1 and 2:1. When this ratio exceeds 7:1, metabolic disorders may arise (National Academy of Sciences, 1984). The Ca/P ratios in Jerusalem artichoke forage were high, ranging from 4.3 to 34.3:1, because of a high Ca concentration and suboptimal level of P. If Jerusalem artichoke were used as the predominant feed, a P supplement or the addition of some other forage with a high concentration of P would be necessary to help reduce the risk of metabolic disorder.

The among-population genetic variance components (σ_g^2) for P and Mg were small, but accounted for the largest portion of the total variance overall (Table 4). The genetic variance for all other elements was higher, with the highest (72.5) for Ca. The ratio σ_g^2/σ_p^2 (genotypic to phenotypic variance) provided an estimate of the proportion of the total variation attributable to population or genetic effects. This ratio is similar to the heritability estimate, but the term heritability is inappropriate because populations are not the progeny of a reference population. The σ_g^2/σ_p^2 ratio was greater than 0.93 for all elements (Table 4), indicating a substantial proportion of the total variation among populations is due to genotypic differences.

The σ_{gy}^2 effect for all elements was low to nonexistent, indicating that the relative concentration of these elements in Jerusalem artichoke was not affected by environment (year). However, the P \times Y interactions for P, Ca, Mg, and the Ca/P ratio were significant and probably

Table 4. Variance components for mineral element concentrations and the Ca/P ratio in Jerusalem artichoke forage from the across-years ANOVA.

Mineral element	Variance components [†] ± SE [‡]				
	σ_g^2	σ_{gy}^2	σ_e^2	σ_p^2	σ_g^2/σ_p^2
N	10.59 ± 4.73	0.0 ± 0.0	0.45 ± 0.01	11.04	0.96
P	0.17 ± 0.07	0.0 ± 0.0	0.01 ± 0.00	0.18	0.94
Ca	72.54 ± 32.31	0.07 ± 0.018	1.04 ± 0.06	73.65	0.98
Mg	0.29 ± 0.12	0.00 ± 0.0	0.02 ± 0.00	0.31	0.93
K	9.12 ± 4.06	0.00 ± 0.0	0.52 ± 0.03	9.64	0.95
Ca/P	100.67 ± 44.83	0.00 ± 0.0	0.06 ± 0.00	100.73	0.99

[†] σ_g^2 = variance due to population; σ_{gy}^2 = variance due to interaction of years and population; σ_e^2 = error variance; $\sigma_p^2 = \sigma_g^2 + \sigma_{gy}^2 + \sigma_e^2$ = phenotypic variance.
[‡] SE of 0.00 indicates SE was < 0.005.

caused by very subtle changes in element concentration and rank. Most elements in Jerusalem artichoke forage appear to be amenable to improvement by selection among the populations. However, P, which is low in forage of Jerusalem artichoke at flowering, has a low population variance and narrow range, so selection to increase this element would not be very effective. Magnesium also has a relatively low population variance component and range.

Variation within Populations

The variance among plants within populations (σ_w^2) was determined for each population in each year for N, P, Ca, Mg, K, and the Ca/P ratio (Table 5). The σ_w^2 within-population variance consisted of genetic variability within populations, plant-to-plant environmental variation, and experimental error. It is reasonable to assume that environmental and error variances are equal for all populations, and differences in σ_w^2 are primarily due to genetic variability within the populations. It seems reasonable to assume that the among-plant environmental variance and experimental error would be similar for clonally (vegetatively) propagated perennial Jerusalem artichoke populations and populations propagated by seed; however, this cannot be tested with the available data. Comparison of σ_w^2 thus provides an

indication of the relative heterogeneity within populations.

There were substantial differences among populations for within-population variability for N, Ca, and K. The within-population genetic variability among populations varied slightly between the two years. The within-population genetic variation of the Jerusalem artichoke populations should allow for the selection of individuals for improving mineral elements in the forage. Again, it appeared as though P, which is low in forage, has a low within-population component making its improvement in a breeding program difficult. Other elements, especially N, Ca, and K, have larger within-population variability and the potential for selection in a Jerusalem artichoke breeding program.

Phosphorus was negatively correlated with N, Ca, Mg, and the Ca/P ratio, but not correlated with K (Table 6). Nitrogen was positively correlated only with K. Calcium was positively correlated with Mg, K, and the Ca/P ratio. Unfortunately, it does not appear to be feasible to select for increased P concentration to reduce the Ca/P ratio to less than 7:1. The high negative correlation between P and the Ca/P ratio ($r = -0.81^{**}$) suggests that the Ca/P ratio could be reduced, but at the expense of a reduced P level, which is undesirable. The narrow range of P concentrations and low variability makes selection for increased P levels unlikely.

Table 5. Within-population variation (σ_w^2) for nine populations of wild Jerusalem artichoke.

Year-population	N		P		Ca		Mg		K		Ca/P	
	Mean	σ_w^2	Mean	σ_w^2	Mean	σ_w^2	Mean	σ_w^2	Mean	σ_w^2	Mean	σ_w^2
g kg ⁻¹												
1983												
Texas-1	15.1b [†]	1.37	1.6b	0.01	9.3h	1.79	2.5f	0.01	16.1c	0.86	5.7h	0.03
Texas-2	12.8c	1.12	1.5c	0.01	13.8g	1.59	2.0h	0.01	14.9d	0.92	9.0g	0.02
Illinois	8.1e	1.54	2.1a	0.02	9.3h	1.58	1.7i	0.01	16.1c	0.92	4.3i	0.23
Minnesota-1	14.9b	1.52	1.1c	0.007	28.6b	3.01	2.6e	0.01	19.7a	1.15	26.6b	0.10
Minnesota-2	7.4f	1.10	0.9g	0.007	22.9c	2.44	3.3a	0.02	10.7g	0.67	24.0c	0.08
Iowa-1	13.0c	1.39	1.0f	0.007	33.8a	3.65	3.2b	0.02	19.2b	1.12	33.7a	0.14
Iowa-2	10.7d	0.25	1.3d	0.008	18.6e	2.09	2.9d	0.02	12.8f	0.75	14.2e	0.04
Iowa-3	15.1b	1.53	1.6b	0.007	21.1d	2.28	3.0c	0.02	13.8e	0.80	13.1f	0.04
South Carolina	16.5a	1.64	0.9g	0.01	16.3f	1.93	2.4g	0.01	12.8f	0.75	17.5d	0.05
1984												
Texas-1	15.3b	0.50	1.7b	0.005	9.8h	0.21	2.6f	0.01	16.3c	0.56	5.8h	0.01
Texas-2	13.0c	0.35	1.6c	0.004	14.5g	0.45	2.1h	0.01	15.1d	0.48	9.1g	0.02
Illinois	8.3e	0.14	2.2a	0.008	9.7h	0.20	1.8i	0.01	16.3c	0.56	4.4i	0.01
Minnesota-1	15.1b	0.48	1.1e	0.002	30.0b	1.90	2.7e	0.01	19.9a	0.84	27.0b	0.15
Minnesota-2	7.6f	0.12	1.0f	0.002	24.0c	1.22	3.3a	0.02	10.8g	0.25	24.3c	0.12
Iowa-1	13.2c	0.37	1.0f	0.002	35.5a	2.65	3.2b	0.02	19.4b	0.80	34.2a	0.24
Iowa-2	10.9d	0.24	1.4d	0.003	19.5e	0.83	3.0d	0.02	13.0f	0.36	14.4e	0.04
Iowa-3	15.3b	0.50	1.7b	0.005	22.1d	1.03	3.1c	0.02	13.9e	0.41	13.3f	0.04
South Carolina	16.8a	0.59	1.0f	0.002	17.1f	0.62	2.5g	0.02	13.0f	0.40	17.8d	0.06

[†] Means in a column followed by different letters are statistically different at $P = 0.05$ according to Duncan's Multiple Range Test.

Table 6. Correlation coefficients (*r*) of mineral element concentrations and the mineral element Ca/P ratio of nine populations of wild Jerusalem artichoke forage harvested at flowering on the basis of data combined for 2 yr.†

Mineral element	P	N	Ca	Mg	K
N	-0.18**				
Ca	-0.66**	0.12			
Mg	-0.59**	0.03	0.71**		
K	0.12	0.36**	0.38**	-0.13*	
Ca/P	-0.81**	0.07	0.95**	0.67**	0.28**

* Indicates significance at the *P* = 0.05 level of probability.

** Indicates significance at the *P* = 0.01 level of probability.

† *n* = 486 for all elements.

The between-population variance (Table 4) and the magnitude of the within-population genetic variance (Table 5) indicate that it should be possible to improve N, Ca, and K concentrations by selecting among and within populations. It may be possible to improve the Ca/P ratio by breeding to lower the Ca concentration of the forage, which is more than adequate already. The variability among the populations for Ca concentration and the low genotype × environment interaction for Ca indicates that this should be possible. However, changing the Ca/P ratio by increasing P concentration does not appear to be possible.

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